

Subalpine fires: the roles of vegetation, climate and, ultimately, land uses

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Abstract Forest fires are controlled by local (vegetation, aspect, elevation, land uses) and regional (climate) factors. The role of these factors remains poorly assessed on centennial to millennial time scales. Here, we investigate fire and vegetation history in five subalpine sites over the past 8000 years to determine when, how, and why there were differences in fire regimes. We focus on time and aspect separately and account for vegetation composition. There are no significant differences in the fire return intervals among sites (~290 years between two fires). The rise of fire frequency from its lowest values (1.5 fires.1000 yr^{-1}) at 8000–7000 years before present (yrBP) to its highest at 4000-3000 yrBP (5 fires-1000 yr⁻¹) is well explained by the high temperatures and low precipitation of the Holocene, both leading to better conditions for fire ignition and spread. From 8000 yrBP, climate is likely the main factor driving the fire frequency on the north-facing sites, which contained mixed Larix decidua-Pinus cembra vegetation; whereas south-facing sites, dominated by the flammable P. cembra and broadleaved trees, appear to be driven by local features, including land use. A shift in the main drivers occurs at 4000 yrBP, when local processes start to control burning activity at all sites. Forest clearance for land use might have directly increased fire frequency, but has also helped to suppress fires through fuel limitation. During the last four millennia, land use likely altered the natural climate-vegetation-fire system mainly by converting forests to grassland by pastoral practices, thus leading to less fire and making the fire-vegetation-climate relationships more complex.

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1 Introduction

Vegetation and fire are closely linked factors with climate. As a result, changes in one factor alter their interactions within this system for centuries, and eventually millennia. Indeed, multiproxy-based analyses have shown the interaction between vegetation and fire frequencies at various single sites since the Lateglacial, but with conflicting interpretations. Some studies at millennial time scales have indicated that fire frequency drives the vegetation composition or abundance (e.g., Genries et al. 2009), while others suggest that vegetation controls the fire frequency and the charcoal load (e.g., Higuera et al. 2009). Alternatively, fire frequency and vegetation can be independent of each other (e.g., Leys et al. 2014), resulting in an inability to make a provable causal link between vegetation and fire history. Comparisons of multiple sites have demonstrated that regional fire history patterns resulted mainly from large-scale processes (e.g., Daniau et al. 2012) that can be temporally overridden by local factors (Gavin et al. 2006; Girardin et al. 2013). This is particularly true in mountain areas, e.g. the European Alps, where landscape fragmentation, resulting from high spatial heterogeneity in relief, soil features, and microclimate, play a chief role in shaping both fire regime and vegetation dynamics over centuries and millennia.

The abovementioned system becomes even more complex when one assumes that prehistoric societies worldwide have altered vegetation composition and fire histories (e.g., (Daniau et al. 2012). In Europe, land use initially transformed the vegetation and landscape patterns, as well as fire regimes, by stimulating or suppressing fires depending on localities and regions (Carcaillet et al. 2009; Rius et al. 2012), due to landscape properties and society skills. Later, during the 19th-20th century transition, forest cover and greater landscape connectivity increased in the European mountains and other low-productivity lands due to abandonment of traditional land uses (Motta et al. 2006). Increases in tree cover and biomass in low-productivity lands were found to induce shifts from fuel-limited to climate-limited fire regimes (Pausas and Fernández-Muñoz 2012; Zumbrunnen et al. 2012). In the next century, the climate is expected to become drier, with longer and more severe summer drought episodes in southern Europe (Giorgi and Lionello 2008), which could alter vegetation flammability and hence fire frequency, severity and area burned (Fréjaville and Curt 2015). A thorough understanding of the likelihood of such scenarios, and their implications, is critical for managing forests and wildfires. Thus, rigorous assessments of potential changes in vegetation and fire regime are needed.

Carcaillet and collaborators (2009) studied four subalpine sites from a single valley but with different modern vegetation assemblages due to heterogeneous historical and local processes (distances from glacial refugia, climate, aspect, soil and elevation), and concluded that a shift in the predominant factors impacting the fire activity appeared around 4500 yrBP. Despite a lack of vegetation data for one site and a sedimentation hiatus covering a period of 2000 yrs in another, the authors assumed a potential social impact as well as presumable differences in the fire histories between sites with a north or south aspect. Because it is useful to better understand human land use history in order to provide suitable management direction in the near future, we stress the need for spatially explicit reconstructions based on local scale observations (Gillson and Marchant 2014; Moritz et al. 2014). Thus, here we provide two new sites to be compared with the three sites published in the Carcaillet et al. (2009)'s study with their local fire and vegetation histories. One studied site (Plan Bouchet) is not included in this analysis, because after verification with an independent lab operator, we discovered that this series was not measured with charcoal but with black shale micro-particles, thus resulting

a major experimental bias. We addressed (i) the historical spatial preference of human activities, (ii) the shift of a climate-induced to a society-driven fire regime and (iii) the change in burned biomass and fuel type through time in response to large-scale processes and local factors. These results are important for planning long-term, sustainable coexistence between societies and ecosystems regularly subjected to fires by providing a better understanding of the extent to which human impacts can catalyse or mitigate the effect of climate variability.

2 Materials and methods

2.1 Study sites

Lac Miroir (unpublished), Lac du Loup (Blarquez et al. 2010b), Lago Perso (Blarquez et al. 2010a), Lac du Lait and Lac du Thyl (Genries et al. 2009) (hereafter Miroir, Loup, Perso, Lait and Thyl, respectively) are lakes situated in dry valleys of the inner western Alps (Fig. 1a, Table S1). These five lakes were chosen because of their small surfaces (<1 ha) and catchment areas (<<1 km²), which allow for precise local reconstruction of vegetation based on plant macroremains (Birks 2003) and fire history (Lynch et al. 2004). Their watersheds are in the subalpine belt with northerly (Miroir and Loup), northeasterly (Perso), and southerly (Lait and Thyl) aspects, and at altitudes of 2214, 2026, 2000, 2196 and 2035 m above sea level (asl), respectively (Table S1). The five small lakes are currently surrounded by various kinds of vegetation resulting from centuries of agricultural land use. Loup, Perso and Miroir are surrounded by forest dominated by *Pinus cembra* L. and *Larix decidua* Mill., with an understorey of ericaceous shrubs and herbs. Multi-century old subalpine grasslands, including, inter alia, *Carex sempervirens* Vill., *Carex curvulea* All., and *Festuca rubra* L., inhabit the watersheds of Lait and Thyl.



Fig. 1 a Location of the five sites: Perso, Loup, Miroir (north facing), Thyl and Lait (south facing). b Principal component analysis (PCA) on presence/absence of plant macro-remains of the five sites. c Point classes defined by the mean and the sd-values of taxa distribution. Each class represents the dispersion on the PCA ordination plot of a site-specific macro-remain assemblage. d is the distance of the axis 1 in the frame

2.2 Sampling and dating methods

Lacustrine sediments were cored with a Russian-corer (1000×75 mm) and the water-sediment interfaces were collected with a Kajak-Brinkhurst gravity corer. Sediments were dated with accelerated mass spectrometry (AMS) radiocarbon measurements and the five sites covered the past 8000 years (Genries et al. 2009; Blarquez et al. 2010a, b). The ¹⁴C measurements <10,000 years before present were calibrated (expressed hereafter in "yrBP") and age-depth models were calculated for each lake (see Fig. S1 for more details).

Sediment cores from each site were sectioned into 1 cm- or 0.5 cm-thick slices for terrestrial plant and charcoal analyses (Table S1). The sites have varying sedimentation rates, thus the time resolution for each sample and site varies accordingly (Table S1). Sample resolutions were standardized using linear interpolated ages to obtain a constant time resolution of 20 yr.sample⁻¹ for all sites, which corresponds to the overall median time resolution.

2.3 Vegetation reconstruction

Terrestrial plant macro-remains used for vegetation reconstruction were extracted by water-sieving (250- μ m mesh size) and identified. The abundances were expressed as accumulation rates (fragments.cm⁻².yr⁻¹) based on macro-remain concentrations and the deposition time determined by age-depth models. Macrofossil assemblages do not fully reflect plant communities, however, plant macrofossils can be extremely informative in the reconstruction of local vegetation histories (Birks 2003) and can be used at least as evidence for the presence of species at a site.

In this study, only the presence/absence of the most common functional taxa were kept for analysis based on the mass-ratio principle indicating that the ecosystem is mediated by the species contributing most to total plant biomass (Grime 1998): needleleaves (*Larix decidua*, *Pinus cembra*, *Abies alba*, *Pinus mugo*, *Pinus* sp. and *Picea abies*) and two broadleaves (*Betula* sp. and *Alnus* sp.). Infrequent taxa were classified by function: "other broadleaves" (*Sorbus* sp. and *Acer* sp.), "shrubs" (*Juniperus siberica*, *Arctostaphyllos uva-ursi*, *Vaccinium myrtillus* and *Vaccinium* sp.) and "herbs" (mainly *Carex* sp.).

In order to highlight differences in plant assemblages through time and space (sites), Principal Component Analyses (PCA) were used with data ordered by taxa. Inter-taxa relationships were inferred from the presence-absence of plant macro-remains in sediments from the sites. The dispersion of classes on the PCA ordination plots delineating site-specific vegetation assemblages demonstrated the relationships among sites. Significant differences of plant assemblages between axis 1 and axis 2 of the PCA, and between classes on the PCA axes were determined with a Kruskal-Wallis rank sum test. The data ordered on component 1 were compared with the data ordered on component 2 of the PCA, representing respectively axis 1 and 2 of the PCA. Then, data ordered on the PCA axes were tested between clusters of site-specific plant assemblages.

2.4 Fire history reconstruction

To reconstruct the fire history, charcoal was extracted from sediments by water-sieving through a 160- μ m mesh. Charcoal area measurements were expressed as charcoal accumulation rate (CHAR, mm².cm⁻².yr⁻¹, Figs. S1 and S2). Because Thyl exhibited a hiatus from ~4500 to

2000 yrBP (Genries et al. 2009), its fire history was not considered from 4500 yrBP to present day.

Fire episodes were reconstructed by decomposing CHAR series into CHAR-background and CHAR-peak components using CharAnalysis v.1.1, with detrended CHAR-peaks representing local fire episodes (Higuera et al. 2010). Reconstructions of fire histories have been recalculated for this paper and were based on locally-weighted polynomial regressions with a similar time window of 700-yr for all sites (Fig. S2). This window maximized the signal-to-noise index (Kelly et al. 2011) and goodness-of-fit between modelled and empirical CHAR distributions (Higuera et al. 2009). All records have to be interpolated to equal intervals of 20 yr.sample⁻¹ to justify the techniques used for peak analysis, which preserves the primary structure of the charcoal data because the resampling technique makes fewer assumptions about the pattern of charcoal deposition within sampling intervals. The ages of the reconstructed local fire episodes were used to calculate fire-return intervals (FRI: years between two consecutive fires, yr.fire⁻¹) and fire frequencies smoothed over a 1000-yr windows (FF: fires per time unit, fires.kyr⁻¹).

Standardized values of FF were averaged following an arithmetical mean (hereafter mFF). A confidence interval (CI) of 95 % was calculated based on percentiles of the distribution of the standardized values of FF. Because FF is typically smoothed over 1000-yr time windows, we also plotted boxplots of mean standardized values of FF at each 1000-yr window. To identify periods sharing the same mFF values, a Kruskal-Wallis rank sum test was applied to the distribution of mFF values between non-overlapping 1000-yr windows.

2.5 Fire history comparisons

Medians and distributions of FRIs from pairs of fire series were compared using Mann-Witney-Wilcoxon, MW (Bauer 1972), and a Kolmogorov-Smirnov, KS, tests (Marsglia et al. 2003). Fire series comparisons were carried out for non-overlapping time windows from 8000 yrBP to present, every 1000 years, then every 2000 years, then every 3000 years, and so on, through the entire duration of the record. Only the relevant time windows are presented in this study, i.e. showing significant differences from one to another in the comparison of fire history. The three time windows retained are the entire duration, from 8000 to 4000 yrBP (period 1) and from 4000 yrBP to present (period 2). Consequently, results report the fire series comparisons between sites and between time periods 1 and 2 for each site except Thyl.

To assess centennial and millennial fire synchronicity between sites, we used a bivariate Ripley's *K*-function modified for time, where each site is a class (Gavin et al. 2006). The *K*-function was transformed to an *L*-function to stabilize the means and variances of *K*-value outputs and facilitate the interpretation of results. CIs of 95 and 99 % were defined for the L(t) values by randomizing 1000 fire events. Each randomization consists of shifting each record a random number of years and wrapping events from the start to the end of the record. Confidence envelopes are set by percentiles in the distribution of the simulated *K*-function. L(t) values >95–99 % CI indicated synchronous fire histories between sites at p < 0.05 and p < 0.01, respectively. L(t) values between the upper and lower CIs indicated independent fire episodes. L(t) values under the CIs indicated asynchrony. For the analysis done using data spanning 8000-0 yrBP, L(t) values were calculated at 100-yr time scales, then every 200-yrs, and so on linearly, to a maximum of 4000 yrs (40 time windows). For the analysis using data spanning 8000-4000 yrBP and 4000-0 yrBP (periods 1 and 2, respectively), L(t) values were calculated every 100 yrs, then every 200 yrs, and so on linearly, up to 2000 yrs (20 time

windows). For instance, for the analysis using data spanning 8000-0 yrBP, the 2000-yr time window of synchronicity analysis represents comparisons of fire event synchronicity between 0–2000, 2000–4000, 4000–6000 and 6000–8000 yrBP. For the analysis using data spanning 4000-0 yrBP, the 2000-yr time window of synchronicity analysis represents comparisons of fire event synchronicity between 0–2000 and 2000–4000 yrBP.

Because some sites present a median time resolution of ~ 30 years (Table S1), we also analysed by the Ripley function fire episodes reconstructed from interpolation intervals of 30 yr.sample⁻¹ (Fig. S5).

Synchronicity in fire events at a large spatial scale suggests that regional processes (i.e. the overall climate of southern Europe), dictate the fire history. Conversely, a lack of synchronicity in fire events suggests that local factors (such as soil characteristics, aspect, elevation, local climatic conditions, vegetation, or land use) predominantly control the fire regime, at different temporal scales. Thus, we expected that a local factor present since 8000 yrs (e.g. elevation or aspect) would lead to asynchrony for the entire period considered, whereas a non-consistent, or changing factor (e.g. human impacts or vegetation turnover) would induce asynchrony at specific moments in the period recorded.

2.6 Paleoclimate data

Summer temperatures and annual precipitation values inferred from pollen reconstructions for four independent subalpine sites in the southwestern Alps (Ortu et al. 2008) were visually compared to the main FF trends. Although other parameterized climate reconstructions are available based on proxy data independent from both charcoal and plant macroremains, they all were derived from sites at lower elevations in the plains, or in northern Europe. The climate reconstruction used in the present study was derived from four independent subalpine sites in the Alps, and thus constituted the most relevant record for a comparison with fire history dynamics at our five sites. The climate data were averaged and expressed as anomalies if corresponding temperature or precipitation values were significantly lower or higher than the means.

3 Results

3.1 Plant assemblages

Taxa distribution on the PCA ordination plot illustrates the differences between plant assemblages (Fig. 1b). Axis 1 of the PCA (PC1, 24 %) is defined by *Alnus sp., Betula sp.*, and other broadleaves and herbaceous plants, and plant macro-remain assemblages from Thyl and Lait (Fig. 1c). Axis 2 (PC2, 19 %) is characterized by *Abies alba*, shrubs, *Pinus mugo*, *Pinus cembra*, *Picea abies* and *Larix decidua* (Fig. 1b), and assemblages from Loup, Miroir and Perso.

According to the Kruskal-Wallis rank sum test, plant macro-remain assemblages are significantly different between PC1 and PC2 (p < 0.01). The KS-test on ordering data among sites also highlighted that Loup assemblages differed significantly from those of Miroir and Perso (p < 0.01, KW-test on PC2 points only) and Thyl assemblages differed significantly from those of Lait (p < 0.01, KW-test on points ordered along PC1). The plant assemblages of Loup and Thyl consisted of specific taxa, i.e. *P. mugo* at Loup, and *Sorbus* and *Acer* clustered in the "other broadleaves" group at Thyl (Fig. S3).

3.2 Fire-return intervals

Over the 8000-year timeframe, 18 fire episodes were detected at Miroir and Lait, the lowest number per time series, with FRI medians of 260 and 320 yr.fire⁻¹, respectively (Fig. S3, Table S2). Perso and Loup experienced more fire episodes, i.e. 34 and 31 fire episodes, respectively, and thus, lower FRI medians, 180 yr.fire⁻¹ (Fig. S3, Table S2). For period 1, Thyl experienced 20 fire episodes, leading to a median of 180 yr.fire⁻¹. Despite these dissimilarities, none of the FRI medians or distributions differed significantly between sites due to large variance (p > 0.05 for MW- and KS-test, Table S3).

The south- (Thyl, Lait) and north-facing sites (Loup, Perso, Miroir) were distinct in their plant assemblages (Fig. 2). However, pairs of FRI medians (MW-test) and distributions (KS-test) for comparison between sites were all similar (p > 0.05, Table S3).

We compared medians and distributions of FRI values between sites for time periods 1 and 2. These comparisons revealed inter-site similarities for both periods (p > 0.05 for MW- and KS-tests, Table S3), and no differences between the two time periods for each site (p > 0.05, Table S2). During period 1, Thyl had the shortest median (140 yr.fire⁻¹, 20 fires reconstructed), and Lait had the longest (300 yr.fire⁻¹, 7 fires reconstructed), thus explaining the lowest *p*-value of the MW-test (p = 0.06, Table S3).

3.3 Ripley analyses: synchrony, asynchrony or independence

L(t) values, calculated based on fire episodes that occurred during both time periods in Loup, Lait, Miroir and Perso (Fig. 2a), fell within the 95 % CI for time scales less than 1500 yr, indicating independent fire episodes between sites for these time scales. However, L(t) values fell above the 95 % CI for time scales between 1500 and 4000 yr, and above the 99 % CI for time scales between 2500 and 4000 yr, indicating synchronous fire episodes.

For north-facing sites (Loup, Miroir, Perso), the L(t) values calculated for 8000 years (Fig. 2b) exceeded the 95 % CI from 400 to 4000-yr time scales, and above the 99 % CI from 1000 to 3800-yr time scales. These sites showed significant synchrony (p < 0.05) on a centennial scale, and highly significant synchrony on a millennial scale (p < 0.01).

L(t) values calculated based on fire episodes at all sites during period 1 fell between the CIs, except for 1000 and 1100-yr time scales, for which L(t) values exceeded the 95 % CI (Fig. 2c), given the significantly synchrony (p < 0.05) on millennial scales and similar FRIs. For period 2, L(t) values fell entirely between the CIs, showing clear independence between local fire histories (Fig. 2d).

Analyses based on slope aspect (north- versus south-facing) and time period yielded more complex results, and different patterns. L(t) values for north-facing sites were synchronous during period 1 at p < 0.05 from 600 to 2000 yr time scales and p < 0.01 at 800 and 1000–1200 yr time scales (Fig. 2e). In contrast, L(t) values were all independent during period 2 for the same sites (Fig. 2f). During the period from 4000 yrBP to present, fire regimes lost their synchrony (period 1), and displayed independence on a centennial time scale. However, L(t) values for south-facing sites during period 1 generally fell within the 95 % CI (Fig. 2g), except with a 700-yr time interval (p < 0.05). This indicates full independence of the fire chronologies between sites for this period, contrary to north-facing sites that appear mostly synchronous.

Because some records have a native sample resolution >20 yr.sample⁻¹, the interpolation interval of 30 yr.sample⁻¹ led to variability in the fire history and the results of the Ripley analyses (Fig. S5). However, despite results less significant (p < 0.05) compared to 20 yr.



Fig. 2 Synchrony of fire episodes between sites (Lago Perso [LP], Lac du Loup [LLo], Lac du Thyl [LT], Lac du Lait [LLa] and Lac Miroir [LM]), assessed by L(t) values transformed by Ripley's *K*-function. L(t) values were calculated based on the 8000-year period for comparisons between: **a** all sites except Thyl and **b** northern-aspect sites only. L(t) values calculated based on the 4000-year period for comparisons between: **c** all sites from 8000 to 4000 yrBP, **d** all sites except Thyl from 4000 to -50 yrBP, **e** northern-aspect sites from 8000 to 4000 yrBP, **f** north-facing sites from 4000 to -50 yrBP, and **g** south-facing sites from 8000 to 4000 yrBP. CI of 95 % (*dashed line*) and 99 % (*dotted line*) were defined for the L(t) values by randomizing 1000 fire events. Each randomization consists of shifting each record randomly in time, and wrapping events from the end to the start of the record. Confidence envelopes are set by percentiles in the distribution of the randomized *K*-function. L(t) values >95–99 % CI indicated synchronous fire episodes between sites at p < 0.05 and p < 0.01, respectively

sample⁻¹ (p < 0.01), and shorter time windows with synchronicity of northern aspect sites, the generalised outcomes are the same.

3.4 Trends of fire frequencies

mFF calculated for all sites (Fig. 3a), and for north-facing sites (Fig. 3b) displayed four distinct periods: (1) an increase from 2 to 4 fires.kyr⁻¹ from 8000 to 6000 yrBP, (2) a stable regime around 4 fires.kyr⁻¹ for all sites, and 5 fires.kyr⁻¹ for north-facing slopes from 6000 to 2250 yrBP, (3) a decrease to 2.5 fires.kyr⁻¹ for all sites from 2250 to 670 yrBP and to 1.5 fires.kyr⁻¹ for north-facing sites from 2360 to 1060 yrBP, and (4) an increasing trend to 4 fires. kyr⁻¹ during the last 500 years.

The lowest mFF of all the sites (1.8 fires.kyr⁻¹) was recorded between 8000 and 7000 yrBP. The highest mFF (4 fires.kyr⁻¹ for all sites, Fig. 3a; and 4 to 6 fires.kyr-1 for north-facing sites, Fig. 3b), occurred between 6000 and 2000 yrBP, peaking between 4000 and 3000 yrBP. The large variance observed between 6000 and 2000 yrBP (Fig. 3a) was dramatically reduced when south-facing sites were excluded (Fig. 3b), but the trend was preserved.

4 Discussion

4.1 Fuel types led to different fire regimes between the two mountain aspects

Due to less solar irradiance, north-facing slopes in the northern Hemisphere exhibit colder temperatures and higher moisture conditions during the growing season, which is limited by longer annual snow retention (Körner 2003). These conditions, combined with bedrock quality (Table S1), were conducive to site-specific establishment and composition of vegetation. Thus, while *Pinus cembra* was present at all sites, *Larix* and shrubs were only present on north-facing sites, and *Betula* and herbs were only present at south-facing sites (Fig. 2).

Among south-facing sites, fire episodes were either independent or asynchronous on centennial time scales (Fig. 2d), and plant assemblages varied significantly (Fig. 1c). This suggests that vegetation differences might have controlled fire ignition and spread, or that other physical features acted on both plant composition and fire history. The south aspect is drier, which should increase vegetation flammability and fire occurrences (Conedera et al. 2004). Indeed, mean FRI of Thyl (140 yr.fire⁻¹; 2035 m a.s.l.) is the shortest for period 1. Thyl assemblages consisted of a higher diversity of woody taxa, notably the presence of broadleaf trees (*Betula, Alnus, Sorbus* and *Acer*, Fig. S3) than Lait assemblages mainly consisting of *P. cembra* and *Betula* (Fig. S3). Varying bark thickness and wood density between broadleaves



Fig. 3 Mean fire frequency (*solid black line*, expressed in fires.kyr⁻¹) surrounded by a 90 % CI (*grey area*) for **a** Perso, Loup, Lait and Miroir, and **b** north-facing sites (Perso, Loup and Miroir). *Boxplots* represent the median, first and third quartiles of fire frequency values at 1000-yr intervals. *Boxplots with different letters* are significant values (Kruskal-Wallis rank sum test, KW-test). Anomalies of **c** summer temperatures (°C), and **d** annual precipitations (mm) derived from four subalpine sites in the southwestern Alps (modified from Ortu et al. 2008). *Dashed grey lines* highlight changes of fire frequencies according to KW-test and at the transition between values under and over the mean on climatic parameters. *Grey zones* correspond to area under the averaged curves of temperature and precipitation values over the mean

and needleleaves induced different combustibility (Frejaville et al. 2013), and fire ignition and spread were closely linked to fuel characteristics, composition and structure. Broadleaves led to higher combustion, due to thinner bark and denser wood than needleleaves. On the other hand, larch wood and bark have the slowest ignition delay, and cembra pines have the highest combustibility (Frejaville et al. 2013). The mixed composition of broad-leaved tree species combined with the flammable cembra pine and the absence of the non-flammable larch at Thyl could explain the higher FF at least during period 1, because pine needles facilitate ignition while wood from broadleaves maintains combustion.

Lait and Miroir, both at the highest elevation (~2200 m, latest departure of growing season) display low fire frequency (Fig. 2a, Table S2) and possess the lowest number of woody species, with *Betula* as the only broadleaf (Fig. S4). Their altitude, rising to the treeline, might explain their low FF, as it makes less woody fuel available due to reduced primary productivity. Moreover, the background charcoal signal of these two sites indicates that charcoal particles are more abundant than charcoal particles of Loup, Thyl and Perso, and their areas are smaller (Fig. S3). High amounts of background charcoal are usually found in non-forested areas, due to high fire frequencies of herbaceous fuel (Duffin et al. 2008; Aleman et al. 2013), and charcoal pieces produced by herbaceous fuel are thinner than those produced by woody fuel source (Jensen et al. 2007). Here, these two sites present significant, distinguishable peaks, both indicating woody fuel presence and allowing fire history reconstruction, but also small pieces of charcoal and high amounts of background charcoal which could indicate higher amounts of herbaceous fuel available compared to Loup, Thyl and Perso, potentially promoting frequent fires. Thus, the fire regime of these sites could have been driven mostly by the fuel available, notably the woody component of the fuel, which is defined as a fuel-limited fire regime.

4.2 Climatic conditions led to an increase in fire frequency from 8000-4000 yrBP

In the previous study of Carcaillet et al. (2009), the pairs of comparisons between sites showed independence of fire episodes over the 8000 years analysed. Here, we found that, during the 8000 years analysed, Lait, Loup, Miroir and Perso sites experienced synchrony in their fire episodes at millennial scale, indicating that fire is mostly driven by long-term regional processes encapsulating all sites (i.e., overall climate of southern Europe). However, at a centennial scale, their fire episodes appeared to be independent. On the other hand, Loup, Miroir and Perso (north-facing sites) displayed synchrony of their fire episodes at centennial to millennial scales, indicating that local factors play a minor role in fire ignition and spread at these sites, and that fire is mainly driven by the regional climate. Thus, the fire history of Lait likely led to an independence of fires at centennial scale. We also found that from 8000 to 4000 yrBP, fire episodes were synchronous on a millennial scale (Fig. 2c) and independent at longer and shorter time scales, contrary to the previous study of Carcaillet et al. 2009. This suggests that local factors acted on fire histories, especially those of the south-facing sites. Then, on a long time scale, regional climate drove the fire hazard in the Alps, while on a short time scale, the fire hazard at Lait or Thyl responded to local drivers. Thus, the fire histories of these two sites are independent.

From 8000 to 4000 yrBP, all sites and north-facing sites recorded an increase followed by a stabilisation of a high mFF (Fig. 3a, b). In the western Alps, the summers of these 3 millennia were drier and warmer than the late Holocene (Fig. 3c), offering optimum conditions for fire ignition and spread. In addition, the vegetation at each site was already established (Fig. S4),

suggesting that the fuel was not a limiting factor for fire ignition. This concordance of favourable factors and the high FF supports the climate-limited fire regime hypothesis. However, the reconstruction of the annual precipitation indicates a wetter climate from 4000 to 500 yrBP (Fig. 3d), co-varying with the highest FF at the north-facing sites at 4000-3000 yrBP, as already reported for Perso (Blarquez et al. 2010a). Although this seems to be counter-intuitive, depending on the mismatch between seasonality of precipitation and the fire season, wetter conditions might increase primary productivity and fuel load in the understorey, thus encouraging fire spread (Zumbrunnen et al. 2009). Particularly in the dry western Alps, it has been reported that the more severe wildfires occurred in winter, which is considered to be the fire season and the season of minimum moisture content in plants (Valese 2007). At the same time, the background charcoal slightly increased, (Fig. S2) and changes in FF were not temporally linked to changes in plant composition, indicating that forest communities were probably productive, and their abundance prevented them from declining, or offered them resilience.

4.3 The last 4000 years: a complex system drove the fire regime

At the onset of the Holocene (11,000 yrBP), western Italian subalpine areas were covered with scattered trees, and between 10,000 and 8000 yrBP the tree cover likely increased until 7000-4000 yrBP (Magri et al. 2015). After, 5000 yrBP, both Loup and Thyl recorded an important decrease in the abundance of tree macroremains, whereas Miroir recorded an increase, especially in *Larix*, around 5500 yrBP (Fig. S3). However, the lack of synchrony in fire episodes, indicating a more prominent effect of local factors, is recorded later than the beginning of vegetation change, at 4000 yrBP (Fig. 2d).

Since 4000 yrBP, deforestations are locally reported in the Italian (Magri et al. 2015) and the French Alps (Genries et al. 2009; Blarquez et al. 2010a, b). Further, human occurrences increased in the inner western Alps (Rey and Thirault 1999) and domestic livestock grazed in subalpine altitudes from the Bronze Age (4100-2700 yrBP) according to environmental DNA evidences (Giguet-Covex et al. 2014). Since the Neolithic, an altered FF in the Alps consisted of fire stimulation (Tinner and Ammann 2005), or suppression (Blarquez et al. 2010b) depending on the land uses. However, we highlight that on south-facing slopes local factors overrode the climate influence on fire episodes and likely controlled the fire regime since 8000 yrBP (Fig. 2g). On north-facing slopes, we found that climate controlled the fire history during period 1, but was followed by a clear shift in dominance of fire ignition and spread from regional processes to local factors ~4000 years ago (Fig. 2e, f). This could be explained by the human settlements found preferentially on the southern exposures, which benefit from a longer growing season and more solar irradiance, both better for pastures and farming (Schwörer et al. 2015). But, the role of climate cannot be ruled out given reported changes around 2500 yrBP to a moister, cooler climate in western Europe (e.g. Van Geel et al. 1996). The FF trend (Fig. 3b) coincides well with the known climate pattern as of 4000 years ago in the western Alps (i.e., wetter and colder; Fig. 3c and d), and human effects on land cover may also contribute.

In the western Alps, mFF decreased from 2500 to 1500 yrBP (Fig. 3a), coinciding with the transition from the Iron Age to the Roman period, which involved increased land use and erosion (Giguet-Covex et al. 2014). This decrease likely eliminated woody plants and expanded grassland for livestock, possibly leading to a change in the fire spread, or a reduction of fire use as a tool for forest clearance. While there is no quantitative evidence of human practices

and population density, over the last millennium, grasslands replaced forest at Thyl and Lait (Genries et al. 2009), and tree density diminished at Loup and Perso (Blarquez et al. 2010a, b). Moreover, the decrease in FF also coincides with the strong decreases in the background charcoal recorded in Lait and Miroir sediment the last 2000 years (Fig. S2, S2), which indicate that there was less and less burned fuel, likely reflecting less available fuel. The last 500 years are marked by a rise in FF. This rise corresponds to an increase in human density and livestock grazing activities; particularly intense in the mid-19th century in the western Alps, but also with drier climate, notably during the Little Ice Age (Casty et al. 2005), which would have favoured vegetation flammability.

Finally, even if no quantitative data support human-induced land use impacts in the western Alps, fire, vegetation, climate and social practices are closely linked, and the well-known fire-climate-vegetation system becomes more complex. This shift, at around 4000–3000 yrBP, from a climate-driven to a society-driven fire regime closely matches fire reconstructions in the Alps, the Pyrenees and the Mediterranean (Colombaroli et al. 2010; Rius et al. 2012; Leys et al. 2014), although at some sites, human impact would have started earlier, at ~7000 cal BP (Keller et al. 2002). More broadly in the northern Hemisphere, the shift in the predominant control of fire regimes, coupled with the increasing human population have modified the fire regimes at ca. 3500-3000 yrBP (Power et al. 2008). In western Eurasia, an increase in fire activity at that time is reported, in contrast to lower fire activity at 6000 yrBP and at present (e.g. Power et al. 2008; Feurdean et al. 2013). We showed with this study that (1) the regional shift appeared at approximately 4000 yrBP in the subalpine belt of the western Alps, and that (2) south-facing sites were already altered by local factors at 8000 yrBP, demonstrating that fire histories in the same region and mountain belt can vary depending on the human preferences in settlements. The key question is not when human impact began, but when and where social practices offset natural processes to control fire regime trajectories and thus, how human impacts can amplify or reduce the effect of climate variability.

5 Conclusion

We compared the fire and vegetation histories of five subalpine sites, highlighting differences in vegetation, aspect, bedrock and elevation. Despite these differences, all sites exhibited similar temporal and spatial patterns of FRI (median) and synchronous fire episodes from 8000 to 4000 yrBP. Nonetheless, fire occurrence was independent among south-facing sites during the period from 8000 yrBP to present, and from the period 4000 yrBP to present for north-facing sites. The general FF pattern aligns well with climate trends, most notably, the first part of the Holocene (8000-4000 yrBP). Consequently, the co-variation of fire frequency and climate parameters suggests regional fire-climate control from 8000 yrBP; but inter-site variations in vegetation and human practices induced independent fire regimes between southern and northern slopes after 4000 yrBP. From 8000 to 4000 yrBP, vegetation experienced an increase in fire frequency at north-facing sites. If future climate changes provoke an increase in fire occurrences within the range of fire regimes reconstructed during this period, this sole process should not alter these subalpine forests. Since 4000 years ago, land use has likely offset the climate-vegetation-fire relationship, causing important changes in the vegetation assemblages by replacing a forest with a grassland system, and by reducing the fire frequency.

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References

- Aleman JC, Blarquez O, Bentaleb I, et al. (2013) Tracking land-cover changes with sedimentary charcoal in the Afrotropics. The Holocene 23:1853–1862
- Bauer DF (1972) Constructing confidence sets using rank statistics. J Am Stat Assoc:687-690
- Birks HH (2003) The importance of plant macrofossils in the reconstruction of lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. Quat Sci Rev 22:453–473
- Blarquez O, Bremond L, Carcaillet C (2010a) Holocene fires and a herb-dominated understorey track wetter climates in subalpine forests. J Ecol 98:1358–1368. doi:10.1111/j.1365-2745.2010.01721.x
- Blarquez O, Carcaillet C, Bremond L, et al. (2010b) Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest. The Holocene 20:139–146. doi:10.1177/ 0959683609348857
- Carcaillet C, Ali A, Blarquez O, et al. (2009) Spatial variability of fire history in subalpine forests: from natural to cultural regimes. Ecoscience 16:1–12. doi:10.2980/16-1-3189
- Casty C, Wanner H, Luterbacher J, et al. (2005) Temperature and precipitation variability in the European Alps since 1500. Int J Climatol 25:1855–1880. doi:10.1002/joc.1216
- Colombaroli D, Henne PD, Kaltenrieder P, et al. (2010) Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. J Ecol 98:1346–1357. doi:10.1111/j.1365-2745.2010.01723.x
- Conedera M, Corti G, Piccini P, et al (2004) Forest fire management in Canton Ticino: attempting a historical overview
- Daniau AL, Bartlein PJ, Harrison SP, et al. (2012) Predictability of biomass burning in response to climate changes. Glob Biogeochem Cycles 26:1–12. doi:10.1029/2011GB004249
- Duffin KII, Gillson L, Willis KJJ (2008) Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity. The Holocene 18:279– 291. doi:10.1177/0959683607086766
- Feurdean A, Liakka J, Vannière B, et al. (2013) 12,000-years of fire regime drivers in the lowlands of transylvania (Central-Eastern Europe): a data-model approach. Quat Sci Rev 81:48–61. doi:10.1016/j. quascirev.2013.09.014
- Fréjaville T, Curt T (2015) Spatiotemporal patterns of changes in fire regime and climate: defining the pyroclimates of south-eastern France (Mediterranean Basin). Clim Chang 1–13. doi:10.1007/s10584-015-1332-3
- Frejaville T, Curt T, Carcaillet C (2013) Bark flammability as a fire-response trait for subalpine trees. Front Plant Sci. doi:10.3389/fpls.2013.00466
- Gavin DG, Hu FS, Lertzman K, et al. (2006) Weak climatic control of stand-scale fire history during the late Holocene. Ecology 87:1722–1732. doi:10.1890/0012-9658(2006)87[1722:WCCOSF]2.0.CO;2
- Genries A, Muller SD, Mercier L, et al. (2009) Fires control spatial variability of subalpine vegetation dynamics during the Holocene in the Maurienne valley (French Alps). Ecoscience 16:13–22. doi:10.2980/16-1-3180
- Giguet-Covex C, Pansu J, Arnaud F, et al. (2014) Long livestock farming history and human landscape shaping revealed by lake sediment DNA. Nat Commun 5:3211. doi:10.1038/ncomms4211
- Gillson L, Marchant R (2014) From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. Trends Ecol Evol 29:317–325
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Glob Planet Change 63:90– 104. doi:10.1016/j.gloplacha.2007.09.005
- Girardin MP, Ali AA, Carcaillet C, et al. (2013) Vegetation limits the impact of a warm climate on boreal wildfires. New Phytol 199:1001–1011. doi:10.1111/nph.12322
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902– 910. doi:10.1046/j.1365-2745.1998.00306.x
- Higuera PE, Brubaker LB, Anderson PM, et al. (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol Monogr 79:201–219
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010) Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. Int J Wildl Fire 19:996–1014. doi:10.1071/ WF09134

- Jensen K, Lynch EA, Calcote R, Hotchkiss SC (2007) Interpretation of charcoal morphotypes in sediments from Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? The Holocene 17:907
- Keller F, Lischke H, Mathis T, et al. (2002) Effects of climate, fire, and humans on forest dynamics: forest simulations compared to the palaeological record. Ecol Model 152:109–127. doi:10.1016/S0304-3800(02) 00011-X
- Kelly RF, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. Quat Res 75:11–17. doi:10.1016/j.yqres.2010.07.011
- Körner C (2003) Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables
- Leys B, Finsinger W, Carcaillet C (2014) Historical range of fire frequency is not the Achilles' heel of the Corsican black pine ecosystem. J Ecol 102:381–395. doi:10.1111/1365-2745.12207
- Lynch JA, Clark JS, Stocks BJ (2004) Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. Can J For Res 34:1642– 1656
- Magri D, Agrillo E, Di Rita F, et al. (2015) Holocene dynamics of tree taxa populations in Italy. Rev Palaeobot Palynol 218:267–284. doi:10.1016/j.revpalbo.2014.08.012
- Marsglia G, Tsang WW, Wang J (2003) Evaluating Kolmogorov's distribution. J Stat Softw 8:1-4
- Moritz MA, Batllori E, Bradstock RA, et al. (2014) Learning to coexist with wildfire. Nature 515:58-66
- Motta R, Berretti R, Lingua E, Piussi P (2006) Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. For Ecol Manag 235:155–163. doi:10.1016/j.foreco. 2006.08.007
- Ortu E, Peyron O, Bordon A, et al. (2008) Lateglacial and Holocene climate oscillations in the South-western Alps: an attempt at quantitative reconstruction. Quat Int 190:71–88. doi:10.1016/j.quaint.2008.04.004
- Pausas JG, Fernández-Muñoz S (2012) Fire regime changes in the Western Mediterranean Basin: from fuellimited to drought-driven fire regime. Clim Chang 110:215–226. doi:10.1007/s10584-011-0060-6
- Power MJ, Marlon J, Ortiz N, et al. (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Clim Dyn 30:887–907. doi:10.1007/ s00382-007-0334-x
- Rey PJ, Thirault E (1999) Le peuplement des vallées alpines au Néolithique: les exemples de la Maurienne et de la Tarentaise (Savoie). Circ identites Cult alpines ala fin la Prehistoire Mater pour une etude (programme Collect CIRCALP 1997, 1998) 501–518
- Rius D, Vannière B, Galop D (2012) Holocene history of fire, vegetation and land use from the central Pyrenees (France). Quat Res 77:54–64. doi:10.1016/j.yqres.2011.09.009
- Schwörer C, Colombaroli D, Kaltenrieder P, et al. (2015) Early human impact (5000–3000 BC) affects mountain forest dynamics in the Alps. J Ecol 103:281–295
- Tinner W, Ammann B (2005) Long-term responses of mountain ecosystems to environmental changes: resilience, adjustment, and vulnerabilityglobal change and mountain regions. In: Huber UM, Bugmann HKM, Reasoner MA (eds). Springer Netherlands, pp 133–143
- Valese E (2007) Wildland fires in the Alpine region of Italy: what's old, what's new. What's next 97-101
- Van Geel B, Buurman J, Waterbolk HT (1996) Archaeological and palaeoecological indications of an abrupt climate change in The Netherlands, and evidence for climatological teleconnections around 2650 BP. J Quat Sci 11:451–460. doi:10.1002/(SICI)1099-1417(199611/12)11:6<451::AID-JQS275>3.0.CO;2-9
- Zumbrunnen T, Bugmann H, Conedera M, et al. (2009) Linking forest fire regimes and climate-a historical analysis in a dry inner Alpine Valley. Ecosystems 12:73–86. doi:10.1007/s10021-008-9207-3
- Zumbrunnen T, Menéndez P, Bugmann H, et al. (2012) Human impacts on fire occurrence: a case study of hundred years of forest fires in a dry alpine valley in Switzerland. Reg Environ Chang 12:935–949